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tive in the Tyndale version in only 44 per cent. of all cases, while *which* has risen from 16 per cent. in Wiclif to 50 per cent. in Tyndale. *Which* was confined largely to nouns and *that* to pronouns. In the eighteenth century, *which* declines in use in the classical English of Addison and Steele, while *that* gains slightly in frequency. A more marked change is manifest in the nineteenth century in the English of Macaulay, where *which* refers to a noun in 99 per cent. of all cases of its use as a relative, constituting a marked feature of his style. In Matthew Arnold, this proportion is preserved; also, though in a less degree, in the writings of Mrs. Humphry Ward. The present tendency is to subordinate the use of *that*, perhaps in part due to its use as a declarative conjunction, while *who* has gained in frequency of use and refers mainly to personal nouns.

Cornell University, Ithaca, April 9, 1904.

OPISTHENOGENESIS, OR THE DEVELOPMENT OF SEGMENTS, MEDIAN TUBERCLES AND MARKINGS *A TERGO*.

BY ALPHEUS S. PACKARD, LL.D.

(Received June 15, 1904.)

Weismann, in his suggestive *Studies in the Theory of Descent* (1876), was the first to discuss the origin of the markings of caterpillars, and to show that in *Deilephila hippophaës* the ring-like spots of the larva "first originated on the segment bearing the caudal horn, and were then gradually transferred as secondary spots to the preceding segments" (Vol. 1, p. 277).

Afterwards (1881-1890), Eimer¹ showed that in the European wall-lizard "a series of markings pass in succession over the body from behind forwards, just as one wave follows another, and the anterior ones vanish while new ones appear behind." He speaks

¹ "Untersuchungen ueber das Variiren der Mauereidechse," *Archiv f. Naturg.*, 1881; "Ueber die Zeichnung der Thiere," *Zool. Anzeiger*, 1882, 1883, 1884; *Organic Evolution*, London, 1890.

of this mode of origin of the markings as the "law of wave-like evolution, or law of undulation." In confirmation of this process or law he cites the conclusions of Württenberger,¹ who had long before (1873) observed that in ammonites all structural changes show themselves first on the last (the outer) whorl of the shell, such a change in the following generations being pushed farther and farther towards the beginning of the spiral, until it prevails in the greater number of the whorls."

Cope, in his *Primary Factors of Organic Evolution* (1896), also shows that in the lizards *Cnemidophorus tessellatus* and *gularis* the breaking up of the striped coloration into transverse spots begins first at the sacral and lumbar regions: "The confluence of the spots appears there first."

We may cite some examples of this law of growth *a tergo*, or opisthenogenesis, as it might be called, which have fallen under our own observation.²

In *Dasylophia anguina*, as shown by the figures in Plate XXI of my monograph of the bombycine Moths, Pt. 1, it will be observed that in stages III, IV and the last stage the dark longitudinal lines become on the eighth to tenth abdominal segments broken up into separate isolated dark spots. In the larva, before the second molt, there are no spots on the ninth and tenth segments. In stage III, however, *i.e.*, after the second change of skin, as stated in my monograph (p. 175), four black spots now appear on the front part of the suranal plate. In the last stage, the reddish spots on the eighth abdominal segment which are detached from the lateral lines of stages I and II, now become specialized into the two black comma-like spots, with a linear spot above and beneath; the two, sometimes divided into four, black spots arise on the suranal plate.

It thus appears that in the ontogeny of this species the process of breaking up or origin of the spots from the longitudinal lines takes place on the last three segments of the body.

In *Symmerista albifrons* the same phenomenon occurs. In stage I, as stated in my monograph (p. 180), on each side of the ninth segment is a large black comma-shaped spot, the point directed forward and downward, while behind there is a median black dot.

¹ *A New Contribution to the Zoological Proof of the Darwinian Theory*, Ausland, 1873, Nos. 1, 2, and *Studies on the History of the Descent of the Ammonites*, Leipzig, 1880 (in German).

² *Proc. Amer. Asso. Advancement Science*, Boston Meeting, 1898, pp. 368-9.

After the first molt there arises behind the dorsal hump two, instead of one, median black spots, and two black spots are added on the side of the body near the base of the anal legs, *i.e.*, two each on the ninth and last segments.

After the second casting of the skin, the marking of the three last abdominal segments becomes specialized; what on the body in front are parallel black and red lines being in this region now represented by separate spots. Thus as regards the marking, the anterior part of the body remains ornamented with the primitive parallel lines; while the process becomes on the three hinder segments accelerated or specialized. It thus appears that the more advanced or ontogenetically later style of ornamentation originates at the end of the body.

A parallel process takes place with the formation of the caudal horn or hump. Thus in *Symmerista*, *Dasylophia* and other horned *Notodontidæ* and members of other groups, the eighth abdominal segment is the theatre of the process of fusion of the two dorsal tubercles of the first larval stage into a single tubercle or horn; so that this segment appears to be the theatre of a process of specialization which does not take place on any other segments of the body.

When in other genera it does take place and there is a specialized single tubercle on the first abdominal segment, as in *Notodonta*, *Nerice* and more especially in *Hyparpax* and *Schizura*, the process of fusion of two tubercles into a single specialized one, as on abdominal segments 1, proceeds from behind forward, as it were in waves of translation of the specialized growth-force from behind forwards.

This may clearly be seen in the figures on Plate XXIV, showing the development of the single hump in *Hyparpax aurora*. In Fig. 1, the dorsal tubercles *i* in stage I are all separated; in Fig. 2, those on the eighth abdominal segment have all begun to unite at their bases before they have on the first abdominal segment; they seem to be a little behind at first, though later on the hump on the first segment becomes higher and larger than the caudal horn.

If there were any doubt as to the relative period when the tubercles become fused in *Hyparpax*, in *Schizura leptinoides* (Pl. XXVI) it is very clearly shown by Fig. 1 that the fusion of the two tubercles forming the caudal hump as we will call it, *i.e.*, that on the eighth abdominal segment, has taken place before any signs

of such fusion have appeared in the pair on any of the segments in front.

When the ontogeny of *Nerice bidentata* is worked out, it will be a matter of much interest to observe whether the dorsal humps are formed from behind forward, or whether they appear simultaneously, and thus form an apparent exception to the law of transfer of growth-force from behind forwards.

In this connection it might be observed that in the larva of *Schizura unicornis*, in which there is the very unusual occurrence of a pair of short thick spines on the vertex of the head (Pl. XXVIII, Fig. 2, 2a, 2b), these spines do not appear in stage I and not until after the first molt. These spines persist through stages II and III, but after this disappear, not being present in the two last stages. Thus the growth-force resulting in the development of the armature of stage I does not reach the head until after the first molt, and then does not persist throughout larval life.

In the ontogeny of the Notodontian family, as well as that of Ceratocampidæ and Saturniidæ, the process of fusion of the two dorsal tubercles always first begins on the eighth abdominal segment.

Opisthenogenesis, as regards the markings, appears to be of a piece, or somehow connected, with the opisthenogenetic origin in post embryonic development of new segments. In the cestodes and in annelid worms, multiplication of segments occurs between the head-region and the extreme end of the body. Thus in *Polygordius*, as stated by Balfour (*A Treatise on Comparative Embryology*, 1880, I, pp. 271, 272), the conversion of the larva into the adult takes place "by the intercalation of a segmented region between a large mouth-bearing portion of the primitive body and a small anus-bearing portion."

This region in the larval or early stages of worms and more primitive arthropods is the "budding zone" of embryologists. While at the outset, in the beginning of embryonic life, the head-region is the first to be formed and the trunk-segments arise later, as in the trochosphere of worms and the protaspis of trilobites and of merostomes, a third portion, arising from the budding zone or seat of rapid cell-formation, appears to be a secondary or inherited region, due to the post-embryonic acquisition of new characters (certain trunk-segments and their appendages) in many segmented or polymeric animals, *i.e.*, those which have passed beyond the trochozoön stage or type.

Prof. E. B. Wilson¹ has clearly stated the nature, now so well known, of the growth-processes involved in the interpolation at the growing point or budding-zone of new segments. In *Polygordius*, after the trochosphere has been formed and when it is about to enter on the adult stages, the segments are formed successively, those in front being the oldest, "while new segments are continually in process of formation, one after another, at the growing point." This, he says, is "a typical case of apical or unipolar growth." It is what we would call opisthenogenetic growth.

Professor Whitman² has shown that in the leech the internal tissues (mesoblast) of the budding zone are arranged in two widely separated lateral bands which, to quote Wilson's exposition, "as the trunk grows older, widen out and grow together along the median line, ultimately giving rise to muscles, blood-vessels, excretory organs, reproductive organs, etc." Now if this is the case with the more important tissues, why in caterpillars as well as in lizards may not this opisthenogenetic mode of growth also involve the arrangement and distribution of the pigment-masses of the integument?

Without entering into the mode of development of the germ-bands, which are behind completely separated, gradually becoming united in front, resulting in their union or concrescence, we would make the suggestion that this phenomenon may be the initial cause or at least in some way connected with the breaking up of the longitudinal stripes of the body, and their transformation into spots at or near the budding zone of their polymeric or polypodous (*Peripatus*-like) ancestors.

In the trilobites, *Limulus* and *Diplopods*, the new segments after embryonic life are interpolated between the penultimate and anal or last segment of the body, and it is from this region in certain *Lepidopterous* larvæ that the transformation of longitudinal stripes into spots takes place. The question next arises whether there is any connection between the opisthenogenetic origin of the markings of lizards and that of caterpillars. The fact, now well established by embryologists, that the phenomena of concrescence occurs not only

¹ *Some Problems of Annelid Morphology*. Biological lectures delivered at the Marine Biological Laboratory at Woods Holl, 1891, p. 61. See also A. D. Mead, "The Early Development of Marine Annelids," *Journal of Morphology*, XIII, May, 1897, pp. 227-326.

² "The Embryology of *Clepsine*," *Journ. Micr. Sc.*, XVIII, 1878; *Journal of Morphology*, Boston, 1887. I am indebted to Prof. A. D. Mead for calling my attention to the concrescence process in this connection.

in fishes but in Amphibia and reptiles, would suggest that the cause of the transformation of longitudinal stripes into spots on the lumbar and sacral regions of lizards is the result of the same specializing growth-force. It may perhaps be regarded as a surviving remnant of the segment-forming force, which has affected the pigment bands in a manner identical in the vertebrates and insects. This transformation of stripes into spots, and the fusion of two dorsal tubercles into a median one, may be, then, the sign of some latent or surviving amount of force concerned in the origin and formation of segments, which crops cut in the larval stages of insects and in young lizards, resulting in this opisthenogenetic mode of origin of spots from bands.

ORTHIC CURVES; OR, ALGEBRAIC CURVES WHICH SATISFY LAPLACE'S EQUATION IN TWO DIMENSIONS.

BY CHARLES EDWARD BROOKS, A.B.

(Read May 20, 1904.)

I propose a study of the metrical properties of algebraic plane curves which are apolar, or, as it is sometimes called, harmonic, with the absolute conic at infinity. If we disregard the right line, the simplest orthic curve is the equilateral (conic) hyperbola, and the name equilateral hyperbola is sometimes extended to orthic curves of higher order. Doctor Holzmüller,¹ who devotes a section to curves of this kind, calls them hyperbolas; and M. Lucas² calls them "stelloides." M. Paul Serret, in a series of three papers in *Comptes Rendus*,³ uses the word "équilatère" for a curve with

¹ *Einführung in die Theorie der Isogonalen Verwandtschaften und der Conformen Abbildungen*, Gustav Holzmüller, Leipzig, 1882, p. 202. . . .

² "Géométrie des Polynomes," Felix Lucas, *Journal de l'Ecole Polytechnique*, 1879, t. XXVIII.

³ *Comptes Rendus*, 1895, t. 121. Sur les hyperboles équilatères d'ordre quelconque, p. 340.

Sur les faisceaux regulieres et les équilatères d'ordre n. p. 372.

Sur les équilatères comprises dans les equations

$$0 = \Sigma_1^{2n-2} l, T_1^n = H_n,$$

$$0 = \Sigma_1^{2n-1} l, T_1^n = H_n + \lambda H'.$$